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PALEONTOLOGY.—Some notes on the Pentameracea, including a description of one new genus and one new subfamily. Thomas W. Amsden, Johns Hopkins University. (Communicated by G. A. Cooper.)

The writer has recently been engaged in a study of the brachiopods belonging to the superfamily Pentameracea in preparation for the forthcoming Treatise on invertebrate paleontology. An investigation of the literature has shown that a new name is needed for the type species of Gypidula and that Barrandella Hall and Clarke is an objective synonym of Antirhynchonella Oehlert. In addition, a study of the collections at the U. S. National Museum has made it possible to add some further information on a previously described genus, Platymerella Foerste, and a previously described species, Pentamerella areyi (Hall and Clarke). A new genus, Costistricklandia, and a new subfamily, Pentameroidinae, are proposed in this report, and a brief discussion of the pentameroid classification, including a list of known genera, is given.

The writer is indebted to Dr. G. A. Cooper for permitting an examination of the collections of the U.S. National Museum and also for valuable suggestions and criticisms during the preparation of this

manuscript.

There has been general unanimity of opinion among the different investigators of the Pentameracea on the importance of the brachial structures in the taxonomy of the group, but there has not been complete agreement on the names to be applied to such structures. The morphologic terms employed in this report (Fig. 1) are essentially the same as those used by Schuchert and Cooper in 1932. In their text figures 26–28 these authors illustrate two distinct types of structure in the brachial valve. One type, which is found in such genera as Conchidium and Pentamerus, shows each

of the brachial plates to be tripartite, consisting of inner plates, brachial process, and outer plates with the last resting directly upon the floor of the valve; the second type, shown in the genus *Pentameroides*, is quadripartite, with each brachial plate composed of inner plate, brachial process, outer plate, and median septum. The writer believes that this terminology accurately describes the brachial structures of the Pentameracea with one exception: namely, the median septum of *Pentameroides* is thought to consist of two plates for which the name septal plates is employed (see discussion of Pentameroidinae).

Schuchert and Cooper applied these names consistently in their systematic descriptions of the various pentameroid genera. However, in their general discussion on the morphology of the Pentameracea (pp. 164–165) they did not use precisely this system but used a modification of Leidhold (1928, pp. 51–53). They state:

The cardinalia of the Pentameridae are the most characteristic feature of the genera and probably of the family as well. These lamellae are divisible into four distinct units termed by Leidhold: (1) The inner crural plate, (2) the outer crural plate, (3) the crural band or border, (4) the septal plate. We prefer to term the first two of these parts simply the outer and inner plates, since we do not feel that it is at present certain that they are the homologues of the crura such as occur in the Rhynchonellacea and Terebratulacea.

For convenience in comparison, two illustrations of Leidhold are reproduced in Fig. 2.

This terminology of Leidhold does not appear to be entirely satisfactory. Although the writer has never examined a specimen of *Gypidula brevirostris*, it would appear

from Leidhold's figure that the "Aussere Cruralplatte" and the "Cruralleiste" represent merely the posterior portion of the brachial process which in this genus is broad and bladelike (see Fig. 1, A). Furthermore, this author used a somewhat different system in describing the genus Enantiosphen (1928, pl. 5, fig. 3). The word "Cruralleiste" was dropped entirely, and "crus" was employed for the structure separating the "Innere Cruralplatte" and platte" and "Aussere Cruralplatte" (and extending on beyond these two plates).

This usage fits in better with the known structure of the pentameroid brachiopods although the writer concurs with Schuchert and Cooper in their desire to drop the word crura in connection with the Pentameracea. It should be noted that the genus Enantiosphen is an unusual pentameroid brachiopod in that the brachial processes terminate in a loop, but at the posterior end the brachial plates which support these processes are pentameroid in their structure and are thought by the writer to exhibit some similarities with the genus Penta-

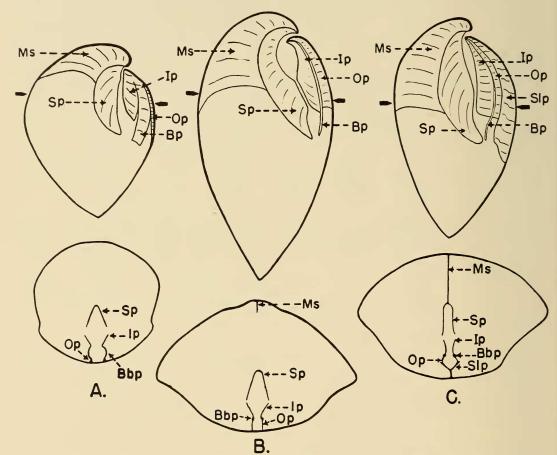


Fig. 1.—Longitudinal (above) and transverse (below) sections showing the internal structure of three subfamilies of the Pentameridae. Heavy, unlettered arrows on longitudinal sections indicate the position of the transverse sections. Transverse sections with pedicle valve above.

A. Gypidulinae. Gypidula coeymanensis prognostica Maynard. Silurian (Keyser), Keyser, W. Va. B. Pentamerinae. Pentamerus cf. P. oblongus Sowerby. Silurian (Clinton), New York. C. Pentameroidinae. Pentameroides subrectus (Hall and Clarke). Silurian (Niagaran), Jones County,

Iowa.

Ms—Median septum Sp-Spondylium Ip—Inner plate Bp—Brachial process Bbp—Base of brachial process Op—Outer plate Slp—Septal plate

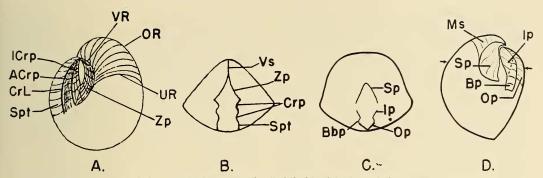


Fig. 2.—Comparison of the terminology used by Leidhold with that of the present paper:

A. Longitudinal section of *Gypidula brevi rostris* Phill. After Leidhold. VR—Vorderrand des ventralen Medianseptums; OR—Oberrand des ventralen Medianseptums; UR—Unterrand des ventralen Medianseptums; ZP—Zahnplatten, das Spondylium bildend; ICrp—Innere Cruralplatte [inner plate]; Acrp—Aussere Cruralplatte [base of brachial process]; Crl—Cruralleiste [junction of brachial process and outer plate]: Spt—Septialplatte [outer plate]

outer plate]; Spt—Septalplatte [outer plate].

B. Transverse section of "Pentamerella" sublinguifer Maur. [Clorinda? sublinguifer]. After Leidhold.
Vs—Ventrales Medianseptum [median septum]; Zp—Zahnplatten, das Spondylium bildend [spondylium]; Crp—Cruralplatten [inner plate plus base of brachial process]; Spt—Septalplatten [outer

C and D. Transverse and longitudinal sections of Sieberella roemeri Hall and Clarke. Silurian (Brownsport), western Tennessee. Arrows on longitudinal section indicate position of transverse section; transverse section with pedicle valve above. Sp—spondylium; Ms—median septum; Ip—inner plate; Op—outer plate; Bp—brachial process; Bbp—base of brachial process.

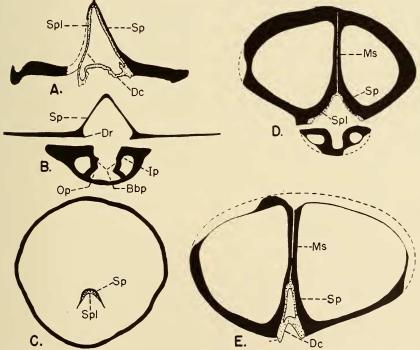


Fig. 3.—Sections showing structures of the pedicle valve. Figures A, B, D, E, after St. Joseph. A. Aliconchidium yassi St. Joseph. Silurian (Hume series), New South Wales.

B. Clorinda undata (Sowerby). Silurian, Norway.

C. Virgiana barrandei (Billings). Silurian (Becsie River), Anticosti Island. D. Pentamerus borealis (Eichwald). Silurian, Norway. E. Pentamerus [?] cf. P. gotlandicus Lebedev. Silurian, Norway.

Bbp—Base brachial process Dc-Deltidial cover

Dr—Delthyrial ridge

Ip—Inner plate

Ms—Median septum Op—Outer plate Sp—Spondylium

Spl—Spondylial lining

meroides. It seems desirable to keep the terminology applied to these two genera as nearly as possible in accord with that applied to other genera in this superfamily.

Accordingly the writer proposes to use the names as employed by Schuchert and Cooper in their text figures 26–28 (with the exception noted above) as being the method which most satisfactorily describes the morphology of this group; it also has the merit of being the system most widely accepted by writers since 1932. (See St. Joseph 1937, pp. 231–254).

The major structure of the pedicle valve is the spondylium which has been rather universally termed a spondylium duplex because of its two fold character. This spondylium duplex may be lined on the inside with a layer of shell material which is different in appearance from the outer wall (Fig. 3). St. Joseph (1937, pp. 240-248) has given a good description of this, finding it to be present in certain species of Pentamerus, Conchidium, Stricklandia and Aliconchidium. This spondylial lining varies in its thickness and in some specimens may extend downwards for some distance as a thin selvage which separates the two layers of the septum (Fig. 3, E). Kozlowski (1929, pp. 124-125, fig. 37) described a similar selvage of material in Sieberella cf. galeata and applied the name "lame intraseptale." The writer has seen a spondylial lining in specimens of Costistricklandia gaspeensis (Billings), Virgiana barrandei (Billings). Brooksina alaskensis Kirk, Stricklandia sp. and Conchidium sp.

St. Joseph (1937, pp. 231–240) noted that in certain specimens of *Pentamerus* the upper edge of this spondylial lining extended across the delthyrium, thus completely closing that opening at the posterior end (Fig. 3, E). This he called a pseudodeltidium and later found it to be also present in *Aliconchidium yassi* St. Joseph (Fig. 3, A).

Kozlowski (1929, p. 130) has also observed that certain species of *Conchidium* and *Pentamerus* may have the delthyrium completely closed by a plate, but he called this a syndeltarium and thought it was formed by the fusion of two plates. Schuchert and Cooper (1932, p. 163) recorded a somewhat similar covering in *Conchidium* and *Har*-

pidium which they preferred to designate by the noncommittal term, deltidial cover. At the present time it is not known how common a structure this is in the Pentameracea. It is apparently always very thin and delicate, and consequently could be easily destroyed; therefore, it may be more universally developed than present knowledge would indicate. Furthermore, the taxonomic significance of such delthyrial covering plates is uncertain at the present time and it would therefore seem advisable to use a noncommittal name such as deltidial cover rather than an expression which implies a homology with a structure in some other group of brachiopods.

There are some pentameroids in which the inner margins of the delthyrium show a thickening or callosity (Fig. 3, B). The significance attached to such structures has varied with different authors, just as it has with the deltidial covers. Hall and Clarke called them deltidial plates and used them to some extent in generic diagnosis whereas Kozlowski (1929, p. 130) applied the name deltarium discretum and considered them to be of ordinal rank. Schuchert and Cooper (1932, p. 163), on the other hand, did not attach much significance to them, noting that they do not close the delthyrium to any notable degree. Structures of this kind which the writer has observed seem to be primarily for the purpose of strengthening the shell margin rather than restricting the delthyrial opening.

# SYSTEMATIC PALEONTOLOGY Gypidula typicalis, n. name

Pentamerus occidentalis Hall, 1858, p. 514, pl. 6, fig. 2; non Pentamerus occidentalis Hall, 1852, p. 314.

The genolectotype (Oehlert, 1887, p. 1311) of Gypidula is Pentamerus occidentalis Hall, 1858, a name that is preoccupied by Pentamerus occidentalis (Conchidium occidentale) Hall, 1852. This homonym has been recognized for many years, but many of the earlier workers thought that Pentamerus occidentalis Hall, 1858, equaled Atrypa comis (Gypidula comis) Owen, 1852. Belanski (1928, pp. 8–9, pl. 2, figs. 1–8), who gave a good description and illustration of Hall's species, noted that there were valid specific differences between Owen's species and that of Hall

but failed to give a new name to the latter. Therefore, it is here proposed that *Gypidula occidentalis* (*Pentamerus occidentalis* Hall, 1858, p. 514, pl. 6, fig. 2; non *Pentamerus occidentalis* Hall, 1852, p. 314) be named *Gypidula typicalis*.

#### Genus Antirhynchonella Oehlert, 1887

Antirhynchonella Oehlert, 1887 (in Fischer's Manuel de Conchyliologie, fasc. xi:1311; non Quenstedt, 1871, pp. 231, 727).

Synonym: *Barrandella* Hall and Clarke, 1893 (pp. 241, 245).

Genotype: Atrypa linguifera Sowerby, 1839 (in Murchison's Silurian System, p. 629, pl. 13, fig. 8).

The status of the generic name Antirhynchonella has been in doubt for a number of years, although it has generally been credited to Quenstedt (type species, tenuistriatus Walmstedt) and suppressed as a synonym of Conchidium. The name was first used by Quenstedt (1871, p. 231) in the following manner:

Aechte Pentameren haben entweder an der Stirn correspondirende Valven, oder Sinus und Wulst ist entgegengesetzt den Rhynchonellen, gleichsam Antirhynchonellen. Selbst die faustgrosse eiförmige tenuistriatus Walmst. auf Gothland, vom Habitus des glatten Esthonus (Eichwald Lethaea ross. I pag. 789) bewahrt diesen markirten Unterschied. Dagegen zeichnen die Engländer einen kleinen glatten Pentamerus linguifer Murch. Siluria 22.21 aus, der seine Zunge entgegengesetzt zur Bauchschale hinauf wendet.

In the index for this publication the name appears as *Antirhynchonella*, but it is not mentioned in the summary of genera and subgenera.

The next usage of the name is by Oehlert (1887, p. 1311), where it is given as Antirhynchonella Quenstedt; it appears as a "section" under Conchidium and is clearly used as a generic name. A diagnosis is given and the type is designated as Atrypa linguifera Murchison (both Quenstedt and Oehlert incorrectly give the author of linguifera as Murchison; it should be Sowerby in Murchison, Silurian System, p. 629, pl. 13, fig. 8).

Hall and Clarke (1894, footnote, p. 245) appear to have been in some doubt as to whether Quenstedt had used the name in a generic sense, pointing out that in the text he employed the name as simply the "Antirhynchonellas" and that it was only in the index that the latin form was applied. Although they were uncertain on this point, they apparently decided to accept it as a valid name but objected to Oehlert's type designation be-

cause, they state: "If any species can be taken as typical of ANTIRHYNCHONELLA, it is Conchidium tenuistriatus, Walmstedt, mentioned in immediate connection with the single use of this name, and not Pentamerus linguifer [a], which is cited by Quenstedt as an illustration of the fact that the position of the fold and sinus in the pentameroids is sometimes the same as in the Rhynchonellas." Hall and Clarke thought that the species tenuistriatus Walmstedt should be referred to the genus Conchidium and proposed to erect a new genus Barrandella for those pentameroid brachiopods having the structure of linguifera Sowerby.

Most later workers have followed Hall and Clarke in this interpretation, regarding Barrandella as a valid genus (linguifera as the type) and suppressing Antirhynchonella (tenuistriatus as type) as a synonym of Conchidium (Schuchert and Cooper, 1932, pp. 173, 181)

It appears to the present writer, however, that the manner in which the latin form Antirhynchonella was published in the index to Quenstedt's book cannot be regarded as acceptable. In the first place there is no evidence that Quenstedt himself was responsible for the appearance of this name in the index to his book, it being just as probable that this entry in the index was due to a misreading of the text passage (p. 231) by another person who compiled the index. Second, even if Quenstedt himself compiled the index and was thus responsible for the appearance of the name Antirhynchonella on page 727, such a method of publication can not properly be held to have provided the name with an "indication" for the purpose of Article 25 (Proviso [a]) of the Rules. The name Antirhynchonella does not appear on the page cited in the index, the only reference on that page which can be held to have any connection with this subject is the vernacular word "Antirhynchonellen." But as long ago as 1907 the International Commission on Zoological Nomenclature ruled (Opinion 1) that a vernacular name is not to be accepted as an "indication." Therefore, the conclusion must be that even if Quenstedt did publish the generic name Antirhynchonella in his index it should be regarded as a nomen nudum.

Under these circumstances the name Antirhynchonella dates from Oehlert, 1887, with the type species Atrypa linguifera Sowerby, 1839, by

<sup>1</sup> The writer is indebted to Francis Hemming, secretary of the International Commission on Zoological Nomenclature, for giving much information and help on this taxonomic problem.

original designation; accordingly Barrandella Hall and Clarke, 1894, becomes an objective synonym. It does not appear to the writer that the suppression of the name Barrandella will cause any great amount of confusion since the genus is not especially common nor does it affect any names above generic rank.

The writer has submitted the foregoing information to the International Commission on Zoological Nomenclature with a request that Antirhynchonella Quenstedt, 1871, be placed on the Official index of rejected and invalid generic names in zoology and that Antirhynchonella Oehlert, 1887, be placed on the Official list of generic names in zoology.

#### Platymerella manniensis Foerste

#### Fig. 4

Platymerella manniensis Foerste, 1909, pp. 70-71, pl. 1, figs. 1A-D; non Platymerella manniensis Foerste, 1920, pp. 223-224, pl. 23, figs. 5, A-H).

The genus Platymerella was proposed by Foerste in 1909, its description being based upon the single species P. manniensis from Silurian strata (Brassfield) at Riverside near Mannie, Tenn. It was distinguished largely upon such external characters as absence of a straight hinge margin, small, subequal beaks and nongaleatiform profile. Foerste noted that the pedicle valve had a short spondylium and septum but did not otherwise describe the internal structure. A few years later Foerste (1920, pp. 223–224), obtained some specimens from the Brassfield at Lawshe, Adams County, Ohio, which he considered conspecific with those from Tennessee. This material included some free interiors of both valves and on this evidence he enlarged his earlier definition and suggested that Platymerella was most closely related to Pentamerella. Foerste's illustrations of the brachial interiors of these Ohio specimens show two distinct types of structure: one shows parallel brachial plates (pl. 23, fig. 5H and ?5G) as in *Gypidula* whereas the other (pl. 23, fig. 5E, 5F) shows a small cruralium. In 1932 Schuchert and Cooper (pp. 184–185) reviewed this genus and referred it to the Pentamerinae rather than the Gypidulinae. They also noted this discrepancy in the nature of the brachial interior and suggested that Foerste may have illustrated specimens belonging to two different genera.

Dr. G. A. Cooper, of the U. S. National Museum, very kindly furnished the writer with a specimen of P. manniensis from the type locality at Mannie, Tenn., which was serially sectioned to show the internal characters. As is shown in Fig. 4, the brachial plates are extremely short with the inner plates extending forward about 3.5 mm and the brachial processes continuing on beyond this as slender, rodlike structures. It is not possible from the material at hand to tell whether the brachial processes are supported at their posterior end by outer plates or whether they attach directly to the valve. If outer plates are present, they are extremely short and are confined to the posterior tip of the shell. The pedicle valve has a thick-walled spondylium duplex which is supported for a short distance by a stout, double-walled septum.

The internal structure of *P. manniensis*, in particular the abbreviated brachial plates, seems to be most like that found in *Stricklandia* and *Costistricklandia*, and it is suggested that *Platymerella* be placed in the family *Stricklandidae*.

The writer has examined Foerste's figured specimens of "Platymerella manniensis" (1920, pl. 23, figs. 5A-H) from Adams County, Ohio, which are at the U. S. National Museum. The brachial valve shown in Fig. 5,H, is believed to be a member of the Gypidulinae, possibly belonging to the genus Gypidula; the specimen shown in 5G is probably the same with the forward portion of the plates broken away. The specimens shown in figures 5E and 5F are more difficult to place but are not believed to be con-



Fig. 4.—Serial sections of *Platymerella manniensis* Foerste ( $\times$  3). Silurian, Brassfield, Riverside near Mannie, Tenn. Peels of these sections at the U. S. National Museum. Pedicle valve above. Distance from posterior tip of pedicle beak: 1—0.5 mm; 2—1.2 mm; 3—1.9 mm; 4—2.1 mm; 5—2.6 mm; 6—3.3 mm.

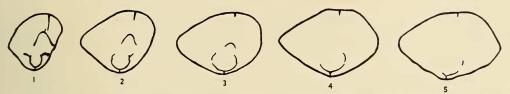


Fig. 5.—Pentamerella areyi (Hall and Clarke) (× 3). Irondequoit limestone, Clinton, N. Y. Peels of these sections at U. S. National Museum. Pedicle valve above. Distance from posterior tip of pedicle beak: 1—2.5 mm; 2—3.1 mm; 3—4.0 mm; 4—4.5 mm; 5—4.9 mm.

generic with *P. manniensis* from Tennessee; they may be fragmentary individuals of a Gypidulinae, possibly *Sieberella*.

#### Pentamerella areyi (Hall and Clarke) Fig. 5

Barrandella areyi Hall and Clarke, 1894, pp. 243, 368, pl. 71, figs. 14-16.

Hall and Clarke based this species upon specimens from the Clinton at Rochester, N. Y. In their description they covered only the external characters, no mention being made of the internal characters beyond noting that the pedicle valve had a well-developed spondylium. Through the courtesy fo Dr. G. A. Cooper, of the U. S. National Museum, the writer obtained a specimen of this species which was serially sectioned. As is shown in Fig. 5, P. areyi has a spondylium which is supported upon a fairly well-developed septum. The brachial valve has long, bladelike brachial processes which are supported upon outer plates that unite before reaching the floor of the valve. Inner plates are also present at the posterior end but these do not extend very far forward.

Hall and Clarke referred this species to Barrandella (=Antirhynchonella), but it differs from that genus in being multicostate. Its characters, both internal and external, are most like those of Pentamerella. P. areyi is considerably smaller than P. arata (genotype), but the external features are similar, both being multicostate and both having a brachial fold and pedicle sulcus. The brachial interiors are similar with the outer plates united to form a cruralium; in P. areyi

these plates unite a short distance above the valve floor to form a double-walled septum. It is only in the pedicle valve that there are some slight differences; in *P. arata* the septum supporting the spondylium is very short whereas in *P. areyi* it extends forward as a complete plate for about a third the length of the valve and is continued beyond this as a ridge.

The reference of this species to *Pentamerella* is interesting because it greatly extends the known range of the genus. In 1932 Schuchert and Cooper (p. 176) gave the range as Middle and Upper Devonian. A few years later Khodalevich (1937, p. 68) described a species, *P. sosviensis*, from the Lower Devonian of the Urals. *P. areyi* extends the range back to the Middle Silurian.

#### Costistricklandia Amsden, n. gen.

Fig. 6

Genotype, Stricklandia gaspéensis Billings, 1859 (pp. 134–135; Hall and Clarke, 1894, pl. 73, fig. 11; Schuchert and Cooper, 1932, pl. 28, figs. 25, 27).

Description.—Shells variable in size but tending to be large with an oval or subcircular outline; hinge line straight, less than greatest width of shell; surface costate. Ventral interior with a spondylium duplex partially supported by a double-walled septum; spondylium usually of moderate length, extending a third or less the length of the valve; both spondylium and septum with thick walls. Brachial interior with long, rodlike brachial processes, which are unsupported by outer plates, their proximal ends attached to

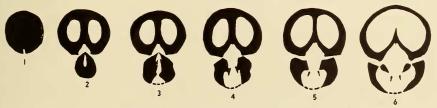


Fig. 6.—Serial sections of Costistricklandia gaspéensis (Billings). (X 1). Middle Silurian, La Vieille formation, Black Cape, Quèbec. Peels of these sections at the Ü. S. National Museum. Pedicle valve above. Distance from posterior tip of pedicle beak: 1—0.9 mm; 2—3.1 mm; 3—3.6 mm; 4—3.8 mm; 5—4.5 mm; 6—5.7 mm.

the posterior end of the valve; at the posterior end the brachial processes are directly overlain by outer plates which extend forward only a short distance.

Discussion.—In 1859 Billings (pp. 132–134) proposed the genus Stricklandia, including within it three English species, Pentamerus lens Sowerby, Spirifer liratus Sowerby, Pentamerus laevis Sowerby, and three Canadian species Stricklandia gaspéensis Billings, S. canadensis Billings and S. brevis Billings. No genotype was designated. A short time later, Billings (1863, p. 370) proposed to replace the name Stricklandia by Stricklandinia under the mistaken concept that his name Stricklandia was invalidated by prior usage for a plant. In 1887 Oehlert (p. 1310) selected S. lens as the genolectotype but almost all later workers have overlooked this and used Hall and Clarke's type designation of S. gaspéensis (1894, p. 251). Since Oehlert's designation clearly has priority over that of Hall and Clarke it must stand as the type.

The original description of Stricklandia lens (Sowerby in Murchison's Silurian System, 1839, p. 637, pl. 21, fig. 3) was based upon specimens from the Llandovery, Carmarthenshire, England. Recently St. Joseph (1937, pp. 323–330, text fig. 20-22, pls. 3, figs. 1-3, 7-9, 12-17; 4, figs. 12, 14; 8, figs. 10-19) has carefully redescribed this species, basing his description largely upon specimens from Norway although he also examined Sowerby's types. The internal characters appear to be very similar to those of Costistricklandia gaspéensis, with both species lacking outer plates; compare St. Joseph's text figures 20 and 21 to Fig. 6 of this report, and also his plate 8, figures 13 and 14, to plate 28, figure 25, of Schuchert and Cooper. The generic distinction between these two genera is based upon external characters, Stricklandia having a smooth shell and Costistricklandia being coarsely costate. They would seem to be closely related to one another and the difference between them is probably comparable to that separating Pentamerus from Conchidium.

Pentameroidinae Amsden, new subfamily

Description.—Rostrate, nongaleate Pentameridae. Pedicle interior with well-developed spondylium duplex. Brachial plates similar to the Pentamerinae but each plate consisting of four rather than three elements: inner plate, brachial process, outer plate, and septal plate.

A single genus, Pentameroides Schuchert and

Cooper, is definitely referred to this subfamily. Two additional genera, *Pentamerifera* Khodalevich and *Conchidiella* Khodalevich, are provisionally included.

Discussion.—The genus Pentameroides was established by Schuchert and Cooper (1931, p. 248; 1932, p. 179) and included only one named species, P. subrectus (Hall and Clarke, 1894, p. 238, pl. 69, figs. 2, 3, 8-10), from the Silurian (Niagaran) of Jones County, Iowa. The writer has recently sectioned two specimens of the genotype which furnish details on the structure of this genus, in addition to the careful diagnosis given by Schuchert and Cooper. As is shown in Figs. 1C and 7, Pentameroides subrectus has a structure which is somewhat unusual for a pentameroid brachiopod. Each of the plates in the brachial valve consists of four elements: inner plate, brachial process, outer plate, and septal plate. These septal plates, which support the other elements, are discrete in their upper portion but unite with each other before reaching the floor of the valve, thus forming a double-walled septum. This structure and the terminology applied to it is similar to that used by Schuchert and Cooper (1932, text fig. 27) with this exception: These authors interpreted the outer plates as resting upon a single plate, the median septum, whereas the writer believes that the outer plates rest upon two plates, discrete at their junction with the outer plates, but coalescing before reaching the valve floor to make a double-walled septum. These are here called the septal plates. (Schuchert and Cooper call this the median septum in text fig. 27, but in the text, p. 165, they use septal plates.)

This structure is in contrast to the other subfamilies in the Pentameridae (Gypidulinae and Pentamerinae) where the brachial plates consist of three elements, inner plates, brachial processes and outer plates. In the Gypinulinae and Pentamerinae these outer plates may be discrete, or they may unit to form a cruralium, but in either case they rest directly upon the floor of the valve. A comparison of these different plate arrangements is shown in Fig. 1.

The terminology as herin used implies or suggests that the inner and outer plates of the Gypidulinae and Pentamerinae are homologous with the same named plates in the Pentameroidinae and that the septal plates of the latter are not developed in the other two subfamilies. Although such an interpretation is not unreasonable, it

can not be regarded as proven at the present time.

It is interesting and perhaps significant to compare Pentameroides with the loop-bearing pentameroid brachiopod, Enantiosphen (Whidborne, 1893, p. 97). The writer has not had an opportunity to examine the internal characters of the latter, but Leidhold (1928, pp. 58-60, pl. 4, figs. 15, 16; pl. 5, figs. 1-3; Torley, 1934, pp. 93-96, pl. 5, figs. 9-10; Cloud, 1942, pp. 144-145, pl. 26, figs. 4-7) has given a good description based upon E. vicaryi (Davidson), from the Middle Devonian of Germany (the original description of this species was based upon specimens from the Middle Devonian of England). Leidhold describes the forward part of the brachial apparatus as consisting of four elements: Innere Cruralplatte, Crus, Äussere Cruralplatte, and Dorsales Medianseptum. The "crura" are overlain by the inner plates (Innere Cruralplatte) and underlain by the outer plates (Äussere Cruralplatte), the latter being supported by the median septum (Dorsal Medianseptum). The "crura" extend extend forward beyond the inner and outer plates to form a loop. This brachial structure, excluding the loop, is similar to that found in *Pentameroides*, a similarity that would be even more marked if the dorsal septum of Enantiosphen could be

shown to consist of a double plate. It seems very possible that further studies of the genus *Enantio-sphen* will show that the Enantiosphenidae and the Pentameroidinae are closely related.

St. Joseph (1937, pp. 286–292, pl. 5, figs. 7–8; pl. 6, figs. 13, 15; text figs. 1, 8) referred a species from the Silurian of southern Norway to Pentameroides (which he treated as a subgenus of Pentamerus). According to his description and illustrations of this species, Pentamerus (Pentameroides) cf. gotlandicus has a structure similar to that of a typical *Pentamerus* except the outer plates join just before reaching the floor of the valve. This author makes no mention of septal plates, nor do his illustrations show such a structure, and it therefore seems probable that the brachial plates of this species are not composed of 4 elements as they are in Pentameroides. Pentamerus (Pentameroides) cf. gotlandicus may represent a new genus which would have about the same structural relationship to Pentamerus that Sieberella has to Gypidula or that Antirhynchonella has to Clorinda. Since the writer has not examined specimens of the Norwegian species, it does not seem desirable to make such a generic distinction at this time.

In 1939 Khodalevich (pp. 96–97; pl. 14, figs.

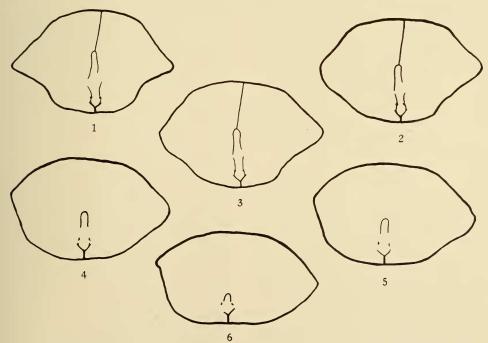


Fig. 7.—Serial sections of *Pentameroides subrectus* (Hall and Clarke). ( $\times$  1.5). Middle Silurian, Jones County, Iowa. Sections at the U. S. National Museum. Pedicle valve above. Distance from posterior tip of pedicle valve: 1—13.5 mm; 2—\$15.5 mm; 3—16.8 mm; 4—18.8 mm; 5—19.5 mm; 6—21.5 mm.

4a-4d; pl. 19, fig. 1) proposed a new genus, Pentamerifera, from the Upper Silurian of the Urals. This genus was described as being externally like Pentamerus and Pentameroides. The plates of the brachial interior were said to be discrete as in Pentamerus, but the structure of each of these plates was compared to Pentameroides, being divisible into inner, outer and septal plates with the brachial process lying between the outer and septal plates. Khodalevich was of the opinion that Schuchert and Cooper were in error when they described Pentameroides as having the brachial process between the inner and outer plates, believing that both Pentamerifera and Pentameroides had the brachial process between the outer and septal plates. The writer's studies of the type species of Pentameroides clearly indicates that Schuchert and Cooper placed the brachial process in the correct position. Therefore, on the basis of Khodalevich's description, the genus Pentamerifera would differ from Pentameroides not only in having discrete septal plates, but also in the position of the brachial process with respect to the other plate elements.

In this same paper, Khodalevich (1939, p. 100, text fig. 17) proposed a second pentameroid genus, Conchidiella. This was said to be internally like Pentamerifera but with external costae. This author figured several transverse sections of Conchidiella which show a structure which appears to have some similarities with the Gypidulinae. Since the writer has not had an opportunity to examine actual specimens of either genus, it is not possible to make any definite observations on the affinities of Conchidiella or Pentamerifera, but they may be provisionally placed in the Pentameroidinae.

#### CLASSIFICATION

In 1932 Schuchert and Cooper placed the following families in the superfamily Pentameracea: Camerellidae, Pentameridae, and Stricklandidae; the family Pentameridae was further divided into two subfamilies, the Gypidulinae and the Pentamerinae. A few years later Ulrich and Cooper (1938) removed the family Camerellidae to the Syntrophioidea, thus leaving only two families in the Pentameracea. The writer is in accord with this revision, but would suggest that the family Enantiosphenidae be included and that the new subfamily Pentameroidinae be added to the family Pentameridae. Following this mod-

ification in classification the superfamily Pentameracea, together with its families and subfamilies, may be diagnosed as follows:

Superfamily Pentameracea. Shells variable in size but tending to be large; commonly strongly biconvex; exterior smooth, costellate, costate or rarely pitted. Pedicle interior with well developed spondylium duplex, usually supported on a double-walled septum, but in a few genera free. Lophophore supports consist of rod- or bladelike brachial processes; these processes unmodified except in the family Enantiosphenidae where they terminate in a loop; at the posterior end the brachial processes are supported on plates, usually extending forward sufficiently to enclose the brachial muscle field (Pentameridae, Enantiosphenidae) but which may be much shortened so as to exclude the muscle field (Stricklandidae). Impunctate.

Family Pentameridae. Smooth, costellate or costate, rarely pitted, Pentameracea with well developed plates supporting the brachial processes; brachial plates may be discrete or may unite to form a cruralium, but in either case they always enclose the brachial muscle field.

Subfamily Gypidulinae. More or less galeatiform Pentameridae, commonly strongly biconvex; fold and sulcus usually present; exterior smooth, multicostate, costate or pitted. Brachial apparatus tripartite, consisting of inner plates, brachial processes and outer plates; brachial processes broad and bladelike; outer plates discrete or coalesced to form a cruralium.

Subfamily Pentamerinae. Pentameridae of moderate to large size with smooth, costate or costellate exterior; fold and sulcus absent or poorly developed. Brachial apparatus tripartite, consisting of inner plates, brachial process and outer plates; brachial processes long and rodlike.

Subfamily Pentameroidinae. Pentameridae with the brachial plates quadripartite, consisting of inner plates, brachial processes, outer plates and septal plates; brachial processes rod-like.

Family Stricklandidae. Large, smooth or costate Pentameracea. Pedicle spondylium thickwalled, supporting septum thick, relatively short. Brachial apparatus with the outer plates much reduced or absent; brachial muscle field not enclosed by brachial plates.

Family Enantiosphenidae. Specialized Pentameracea in which the brachial processes terminate in a loop; supporting plates quadripartite, consisting of inner plates, brachial processes,

outer plates and? median septum (or? septal plates).

The following list includes all the pentameroid genera known to the writer at this time:

Superfamily PENTAMERACEA Schuchert, 1896 Family Pentameridae McCoy 1844

Subfamily GYPIDULINAE Schuchert and Le-Vene, 1929

Gypidula Hall, 1867 Sieberella Oehlert, 1887

Pentamerella Hall, 1867

Antirhynchonella Óehlert, 1887 (syn. Barrandella Hall and Clarke).

Clorinda Barrande, 1879

Salonia Cooper and Whitcomb, 1933

Wyella Khodalevich, 1939 Clorindina Khodalevich, 1939 ? Metacamerella Reed, 1917

Subfamily Pentamerinae Waagen 1883

\* Pentamerus J. Sowerby, 1813

\* Conchidium Oehlert, 1887 [= Conchidium "Linnaeus" of Authors]

Capelliniella Strand, 1928

Lissocoelina Schuchert and Cooper, 1931 Rhipidium Schuchert and Cooper, 1931

Harpidium Kirk, 1925 Brooksina Kirk, 1922

Cymbidium Kirk, 1926

Aliconchidium St. Joseph, 1942

? Notoconchidium Gill, 1951

? Zdimir Barrande, 1881

Subfamily Pentameroidinae Amsden, new Pentameroides Schuchert and Cooper, 1931

? Conchidiella Khodalevich, 1939

? Pentamerifera Khodalevich, 1939

Family Stricklandidae Hall and Clarke, 1894 Stricklandia Billings, 1859

Costistricklandia Amsden, n. gen.

Platymerella Foerste, 1909

Holorhynchus Kiaer, 1902

? Virgiana Twenhofel, 1914 Family Enantiosphenidae Torley, 1934

### Enantiosphen Whidborne, 1893 REFERENCES

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<sup>\*</sup>The status of the generic names *Pentamerus* and *Conchidium* is uncertain. E. S. Alexander (1951) has submitted a petition to the International Zoological Commission on Nomenclature to have these names added to the official list of genera.